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## Ethospecies, Ethotypes, Taxonomy, and Evolution of *Apicotermes* and *Allognathotermes* (Isoptera, Termitidae)

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The present paper is a sequel to an earlier report on the genus *Apicotermes* (Emerson, 1953). Two new species of *Apicotermes* are here described, notes on comparative anatomy of the known species are included, and one species formerly included in *Apicotermes* is transferred to the closely related genus *Allognathotermes*.

Grassé and Noirot (1954) have contributed a fine study of *Apicotermes arquieri* and its nest structures together with related genera and their constructions. Their pioneer discovery of interesting taxonomic characters in the intestines of the workers and soldiers opens up a new field of phylogenetic study that should be more fully exploited in the near future.

Our knowledge of the taxonomy and nest structures of *Apicotermes* is growing rapidly and has already furnished us with an outstanding illustration of the phylogeny of behavior among animals (Schmidt, 1955a,

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1955b). New specimens and new observations are filling in many gaps in our information, but many intriguing problems are unsolved as yet, so that each new study is at best only a small step towards a more adequate and comprehensive appraisal of the biological principles already suggested. Much more collecting as well as field and laboratory study of the living insects is needed.

*Apicotermes gurgulifex*, new species

"Nid I" DESNEUX, 1918, p. 299, figs. 1, 2 (nests).

"*Apicotermes* sp. ? (Sankuru et Kisantu)" DESNEUX, 1948, pp. 7, 15-16, pl. 5, figs. 1-3, pl. 7, fig. 1 (nests).

"*Apicotermes* sp." EMERSON, 1949, in Allee *et al.*, p. 633, fig. 231 (nest).

"Nest from Kisantu" EMERSON, 1952, p. 342, fig. 28 (nest phylogeny).

"Nid à gargouille" DESNEUX, 1953, pp. 23, 25, 38, 77, 81, 88, fig. 8, pls. 13, 15 [1] (nests).

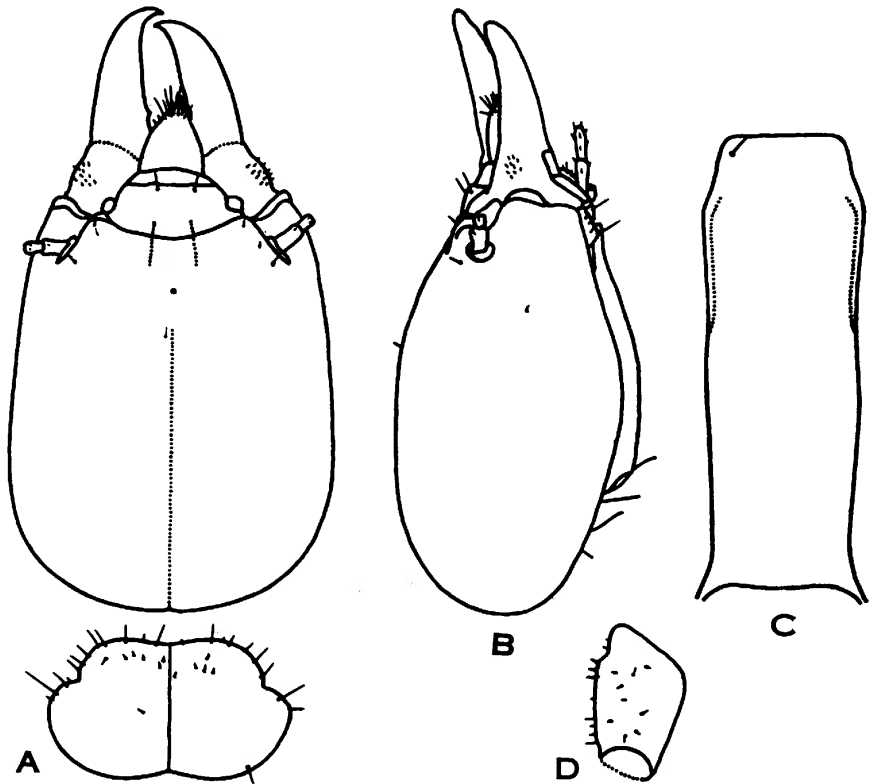


FIG. 1. *Apicotermes gurgulifex*, new species, holotype soldier, Lunda, Angola. A. Head and pronotum from above. B. Head from the side. C. Enlarged postmentum from below. D. Coxa of foreleg showing profile of ridge.

*Apicotermes gurgulifex* EMERSON, 1955, in Schmidt, 1955a, p. 164 (soldier).

*Apicotermes gurgulifex* SCHMIDT, 1955a, pp. 160, 161, 164–167, 169, 171, 173, figs. 1–4, table 1 (nests).

*Apicotermes machodoensis* WEIDNER, 1955, p. 204, fig. 10 (nest).

*Apicotermes gurgulifex* SCHMIDT, 1955b, pp. 347, 349, 352 (nest).

The nest structures of this species (fig. 3) have long been known and are described, figured, and discussed in numerous publications.

SOLDIER (FIG. 1): Extremely close to *Apicotermes desneuxi* Emerson. The profile of the top of the head is fairly evenly convex between the front and the vertex (fig. 1B). Two paratype soldiers in the author's collection from the type colony of *A. desneuxi* from the Inkisi region, Belgian Congo, and one paratype soldier of the same species from Leopoldville, Belgian Congo, have an angle between the front and vertex

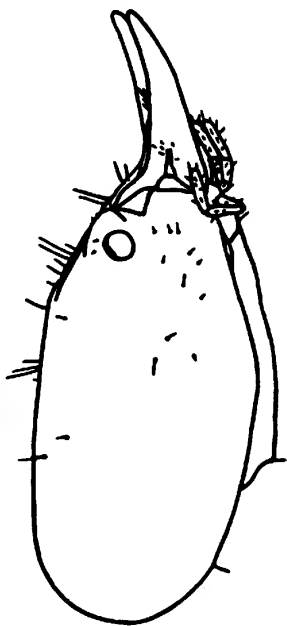


FIG. 2. *Apicotermes desneuxi* Emerson, paratype soldier from type colony, Inkisi region, Belgian Congo. Head from the side.

and the top of the head is flatter in profile (fig. 2). Otherwise *A. gurgulifex* closely resembles the description, drawings, and measurements of *A. desneuxi* (Emerson, 1953, pp. 108–113). Some of the bristles on the dried holotype specimen of *A. gurgulifex* were probably rubbed off. The postmentum, pronotum, and front coxa are closely similar to those of *A. desneuxi*. The differentiating morphological character of the head

shape is only tentatively of taxonomic value and possibly may be within the normal range of variation of *A. desneuxi*.

TABLE 1  
MEASUREMENTS (IN MILLIMETERS) OF SOLDIER OF *Apicotermes*  
*gurgulifex*, NEW SPECIES

	Holotype, Lunda	Paratype, Dundo
Length of head with mandibles . . . . .	4.63	3.80
Length of head to side base of mandibles . . . . .	3.21	2.70
Width of head . . . . .	2.51	2.10
Thickness of head . . . . .	1.77	—
Length of postmentum . . . . .	2.04	1.60
Widest width of postmentum . . . . .	0.73	0.59
Narrowest width of postmentum . . . . .	0.67	0.44
Length of left mandible . . . . .	1.81	1.50
Length of pronotum . . . . .	0.96	0.90
Width of pronotum . . . . .	1.94	2.00
Length of hind tibia . . . . .	1.96	—

WORKER: The condition of the specimens is poor, but they seem to be close to those of *A. lamani* in the leg characters. Comparisons of workers of various species are contained in the discussion on the phylogeny of the species towards the end of this paper.

DISTRIBUTION AND ECOLOGY: The single dried holotype soldier was found by W. V. Harris together with workers in a nest structure (fig. 3) collected by A. W. Exell at Lunda, near Vila Henrique de Carvalho, Angola, April, 1937, in sandy soil. Both the holotype soldier and the nest structure are deposited in the British Museum (Natural History). H. Weidner sent specimens of the paratype colony from Dundo, Angola, collected by A. de Barros Machado.

Nests that seem surely to belong to this species are recorded from Kondue (Sankuru region), Mayidi (near Kisantu), and Plateau de Kamina (Lualaba) in the Belgian Congo (all in the Musée Royal du Congo Belge, Tervuren) and from Haut Zambèze in Angola. No associated termites are known except the specimens mentioned above. Weidner (1955, p. 204) figures a nest from Dundo, Angola, constructed by *Apicotermes gurgulifex*. He assigned the nest to *A. machodoensis*, new species, but has generously sent me soldier measurements and has allowed me to include his material as a paratype colony under the name of *A. gurgulifex*.

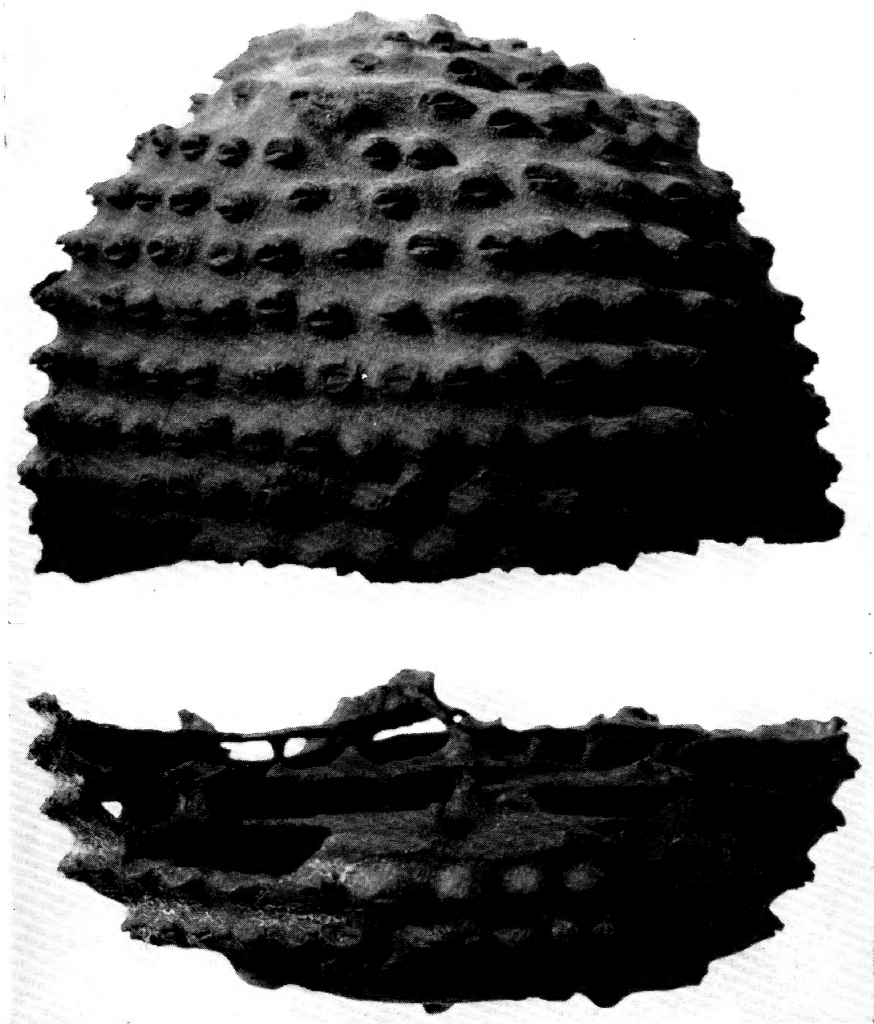


FIG. 3. *Apicotermes gurgulifex*, new species. Portions of nest of type colony, Lunda, Angola.

#### THE CONCEPT OF THE SPECIES AND THE ETHOSPECIES

It is noteworthy that the assignment of the nests that are the product of the behavior of the workers of *Apicotermes gurgulifex* to the genus *Apicotermes* by Desneux (1948) implied a prediction that the soldier associated with the workers would prove by anatomical characters to belong to an undescribed species of the genus. This foresight is ade-

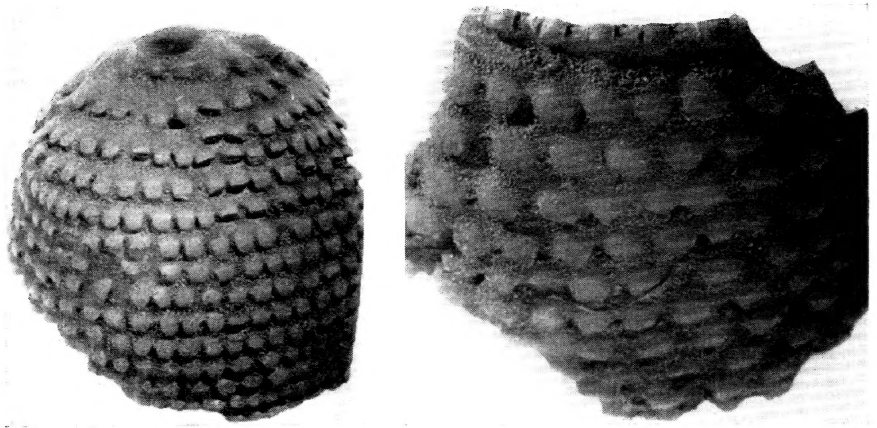


FIG. 4. *Apicotermes desneuxi* Emerson. Portions of nest of type colony, Inkisi region, Belgian Congo. Photograph courtesy of Dr. J. Desneux.

quately substantiated by the morphology of the soldier here described.

The characters that distinguish *A. gurgulifex* from *A. desneuxi* are principally ethological. The surface of the nests illustrated by Desneux (1948, 1953), Schmidt (1955a), and in figures 3 and 4 shows a clear separation, although the simple pores through the nest walls of these two species are homologous and obviously related. The structure of the single dried soldier, taken from a nest (fig. 3) closely resembling the "nid à gargouilles" of Desneux, is so close to that of *A. desneuxi* (fig. 2; Emerson, 1953, pp. 108–113, figs. 2C, 4A) that the author probably would have erroneously placed it under *A. desneuxi* were it not for the nest differences. The evenly convex profile of the front and vertex of the head (figs. 1B, 2) is the only morphological difference detected from the six soldiers known from the type colony (Inkisi region, Belgian Congo) and the two soldiers known from the paratype colony (Leopoldville, Belgian Congo) described as *A. desneuxi*. This character may not prove to be qualitative when many specimens of both species are studied. However, it is also possible that statistically significant quantitative differences between the two species may be discovered when sufficient numbers of specimens become available. This proved to be the case for the closely related "physiological species" *Nasutitermes guayanae* (Holmgren) and *N. similis* Emerson (Emerson, 1935) which were distinguished at first only by the different species of associated termitophilous beetles.

It is most likely that distinctive characters will be found in the soldier caste rather than in the morphologically more conservative reproductive

or worker castes. It should be pointed out, however, that the ethological distinctions are most clearly seen in the nest-building behavior of the worker caste which seldom exhibits morphological distinctions of much value for species diagnosis within the same genus. The worker caste is not only responsible for the behavior characters in the nests of the various species of *Apicotermes*, but is responsible also for the ecological and physiological responses of the host-specific termitophiles resident in the nests of various genera.

With such close anatomical resemblance and the present dearth of specimens for adequate statistical analysis, it may be argued that the ethospecies, *Apicotermes gurgulifex*, should not be named. The author (Emerson, 1945, 1955) believes that the species concept should follow genetic distinctions of reproductively isolated natural populations. In the case of *A. gurgulifex*, the ethological distinction of the nest structure is surely genetically induced and is a remarkable example of instinctive behavior of a colony population, an ethological character that passes from one colony to another through the germ cells of the reproductives that do not exhibit the behavior in their individual lives. Among the known species of the genus, the correlation of the distinctive morphological and ethological characters is complete, so that no reasonable doubt exists that most *Apicotermes* species are distinctive in both their ethology and morphology, although the remarkable nest structures offer more detailed specific characters than does the anatomy of the soldiers or reproductives (Desneux, 1953; Emerson, 1953; Schmidt, 1955a). The imago caste is now known for four named and one unnamed species of *Apicotermes*. There are detectable differences between the imagoes of the different species, but the soldier caste is more distinctive and possesses more structural characters that indicate relationship, particularly between pairs of species. The imago caste is taxonomically more conservative than the soldier caste in the large majority of termite species, although there are a few exceptions (i.e., *Reticulitermes*), so it is to be expected that adequate statistical differences of structure between *A. desneuxi* and *A. gurgulifex* will be found more easily in the soldier caste.

In the comparison between *Nasutitermes guayanae* and *N. similis* (Emerson, 1935), the soldier showed overlapping quantitative differences, but the imagoes were not anatomically distinct. It is still uncertain whether *N. columbicus* (Holmgren) deserves specific separation from *N. guayanae* (Holmgren). No morphological distinction has been detected for either the soldiers or the imagoes, and some species of phylogastric termitophilous Staphylinidae are the same in the nests of both *N. guayanae* from British Guiana and *N. columbicus* from Panama.

When a more adequate study of these specimens has been made, it may result in placing *N. columbicus* in synonymy with *N. guayanae*. However, it is highly improbable that the validity of the species distinction between *N. guayanae* and *N. similis* can be demolished. Some additional data from both termite hosts and termitophiles since the published statistical study (Emerson, 1935) corroborate the hypothesis of genetic physiological distinctions between the host species of termites to which the termitophiles react. The specific separation of *N. guayanae* and *N. similis* has been questioned by Thorpe (1940, p. 347) and Borgmeier (1950, p. 629) on grounds that, in the opinion of the author, have slight biological foundation.

It should be emphasized that nothing is known directly of the genetic distinctions of any species of termite, but it may logically be assumed that multiple genetic differences separate species that are reproductively isolated. Coexistence of sympatric species without overlapping characters that would indicate interbreeding in the same geographical region and in closely similar ecological niches is circumstantial evidence for reproductive isolation. It is known that *N. guayanae* and *N. similis* occur together in the same locality (Kartabo, British Guiana) and in the same ecological niche (arboreal nests in lowland tropical rain forest). The geographic ranges of the species are probably somewhat different. The data at present do not indicate what, if any, geographical or ecological isolation there may be between *Apicotermes desneuxi* and *A. gurgulifex*. It may be presumed that *Nasutitermes guayanae* is intrinsically isolated from *N. similis*. There is no evidence for or against the postulate that *Apicotermes desneuxi* is intrinsically isolated from *A. gurgulifex*, although the distinctions of the nests suggest no gene exchange between the species.

It is to be expected, particularly following the interpretation of Muller (1942), that species will diverge with the accumulation of multiple genetic differences following the complete cessation of gene interchange caused by geographical, ecological, ethological, physiological, or sexual separation. The genetic divergences affect physiological characters that in turn may affect morphology or behavior. Anatomical characters are used predominately by taxonomists because of their utility in describing and relating species. But other systems may also be sensitive to the genetic divergence, and in a few instances the distinguishing characters may be detected more easily by physiological, ethological, or ecological responses. It is not to be expected that a high percentage of species exist that do not show anatomical distinction from their closest relatives, so taxonomists need not be overly concerned that the basic data on which



their science rests are unsound in principle. However, they should recognize the possibility that an occasional species may not exhibit easily detected morphological distinctions, even though anatomic structure is usually extremely sensitive to slight genetic and physiological differences and consequently may be expected to be correlated with evolutionary processes in the vast majority of cases.

Schmidt (1955a, pp. 165–166) discusses and diagrams somewhat different nest conduit construction for *Apicotermes kisantuensis* I and II and for *A. angustatus* A and B, taking his data in large part from Desneux (1948, 1953). These slight differences in ethological characters have not been correlated with any anatomical differences in the termite soldiers associated with these nest types. Both Desneux and Schmidt suggest the possibility that more than one species, subspecies, or race of termite may build these different nest types. Until further taxonomic information is gathered, I suggest that these termites be referred to as “ethotypes” with indications of racial differences in their respective genetic behavior but, with our present information, without taxonomic nomenclatural status. The term “ethotype” parallels, for genotypical behavior distinctions of races, the term “ectotype” used by Turesson (1922) for the genotypical response of a population to a particular habitat. With further data, the ethotypes of *A. kisantuensis* and *A. angustatus* may prove to be ethological subspecies or species, depending upon the indicated partial or complete reproductive isolation of the populations.

It has now been established experimentally (Light, 1942–1943, 1944; Miller, 1942; Lüscher, 1952; and Grassé, 1952) that the castes of termites are not genetically determined, but that differential caste development is the result of different physiological induction mechanisms operating upon similar genetic foundations. There is probably some Mendelian segregation in the different individuals of a colony with a single royal pair, but these individual genetic differences have no correlation with the potential ability of any single individual to develop into a reproductive, a soldier, or a worker. Therefore, it may be assumed that the worker that cooperates with other workers in the construction of a specific type of nest, such as that formed by the workers of *Apicotermes gurgulifex*, has no correlated genetic difference from the adult soldier or reproductive, although the anatomy and the behavior of the worker differ markedly from those of the other castes. One must conclude from the data on caste development that physiological “triggers” or “graded effects” release or inhibit the determining mechanisms for the development of each caste, including the ethological as well as the anatomical

caste characters. These "triggers" or "graded effects" may be biochemical agents or "exohormones" produced by physiological, ecological, or ethological stimuli.

Different somatic tissues of a single individual organism usually have equivalent genetic patterns passed along by equational mitosis, and ontogenetic tissue differentiation within the same individual is the result of physiological distinctions in the developmental processes. This fundamental principle of tissue differentiation is analogous to the similar principle involved in caste differentiation from genetically similar eggs in the termite colony. Thus the whole colony is analogous to the whole individual organism in certain basic biological characteristics and may be referred to as a social "supraorganism" (Emerson, 1952). With the modern advances in psychosomatic correlations in the human species, we must allow for the probability that physiology and behavior interact in both directions with many "feed-back" effects. Such biological correlations of anatomy, physiology, and behavior seem to negate a philosophy of dualism with its concept of independence of body from psyche.

Of importance in the interpretation of the taxonomy and evolution of *Apicotermes* is the fact that the workers integrate their individual behavior to produce a function of the group as a whole with a social psychological pattern difficult to detect in the individual psychology of each worker. The psycho-biological manifestations of the group system indicate "emergent" attributes not found in the individual workers acting alone. The sterile castes have evolved caenogenetic specializations of immature stages (Emerson, 1949, in Allee *et al.*, p. 635), and the worker termite parallels the taxonomic difficulties found in the nymphal stages of paurometabolous insects. The caenogenetic evolution of the sterile castes of termites may be contrasted to the deutero-genetic evolution of the sterile castes of the social Hymenoptera. It seems obvious that one tissue within the same individual organism may be more sensitive than another to genetic and evolutionary change, and that one caste within the social supraorganism may also exhibit evolutionary conservatism in some directions at the same time that it exhibits functional specialization in other directions. It is also apparent that the adaptive behavior and anatomy of a sterile caste evolve without a Lamarckian influence (Emerson, 1949, in Allee *et al.*, p. 599).

*Apicotermes gurgulifex* seems best interpreted as a distinct species primarily distinguished from *A. desneuxi* by ethological characters exhibited in the nest construction (figs. 3, 4). This hypothesis must remain somewhat tentative until more specimens are collected and studied statistically. The data already gathered, however, make the hypothesis of a pair

of ethospecies the most probable, and the information is here presented to fill partially an important gap in the systematics and phylogeny of the genus *Apicotermes*. As has already been stated in several publications, including Schmidt (1955a), *Apicotermes* nest structures are the best material as yet available to indicate that phylogeny of behavior parallels in principle that of anatomical structure and that the adaptive divergence together with the regressive evolution of vestigial characters is caused by similar evolutionary processes affecting both the morphology and the ethology. The functional anatomy and the functional behavior are probably genetically both somewhat independent and somewhat dependent on each other. Modern biological investigations of the basic principles of evolution, taxonomy, genetics, physiology, development, behavior, and ecology show that these fields of inquiry are all related and together indicate fundamental resemblances of living processes even though specialists by necessity use different techniques to indicate various facets of life. No one field of biology is either wholly independent of or more fundamental than another. Genetics initiates physiological development that in turn influences the growth of structure or the action of the nervous system. But the functions of the structure, behavior, or physiology of the organism or supraorganism in its complex environment determine its survival, so that ecological relations in turn determine the genetic patterns through natural selection. Life processes have circular or web causation and many "feed-back" mechanisms exist in both ontogenetic and phylogenetic time. The effect influences the continuous or repeated cause. *Apicotermes gurgulifex* is a remarkable example illustrating some of these interrelationships of the phenomena of life. Certain details and a more extensive discussion of relevant facts and their interpretation may be obtained by reference to Desneux (1948, 1953); Allee, Emerson, Park, Park, and Schmidt (1949); Tinbergen (1951); Emerson (1953); Grassé and Noirot (1954); and Schmidt (1955a, 1955b).

The concept of a phylogeny of behavior of *Apicotermes* supplements the studies of Emerson (1938) on termite nests, of Lorenz (1941) on duck behavior, and of Tinbergen (1951) on instinct. Another instance of ethospecies with close morphological similarity is cited by Adriaanse (1948). Lehrman (1953) questions the genetic basis of "instincts." The data and interpretations of the present study of ethospecies and the phylogeny of behavior seem to the author to be at variance with Lehrman's position, although the term "instinct" has a historical ambiguity and has been used by different authors with different meanings. If genetically induced behavior is not called instinctive, we must find another more precise term for this fundamental type of behavior. Doubtless

much behavior of insects may be learned or conditioned by experience, but there is also no doubt that such behavior as that exhibited by the different species of *Apicotermes* in the construction of their nests, and by 245 named species in nine genera of Macrotermitinae in the construction of their fungus gardens, is induced by factors passed from generation to generation through the fertilized egg. The single exception (*Sphaerotermes sphaerotherax*) among the fungus-growing termites (Grassé and Noirot, 1948) is probably another case of vestigial behavior that is analogous to the vestigial behavior exhibited by the nests of *Apicotermes occultus* and *A. arquieri* (Schmidt, 1955a). Organic evolution of either anatomical structure or behavior always is an evolution of genetic systems.

*Apicotermes holmgreni*, new species

QUEEN (FIG. 5): The head and pronotum are brownish black, with light dots at the base of the bristles and hairs on the head, thorax, and abdomen. Postclypeus with a median dark longitudinal line. Pronotum

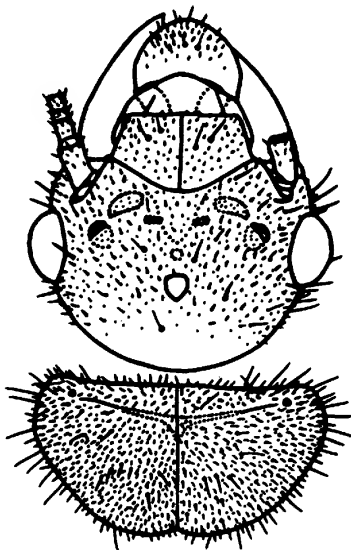


FIG. 5. *Apicotermes holmgreni*, new species, morphotype queen, near Nsakar Hill, Nyasaland. Head and pronotum from above.

with a broadly Y-shaped groove, the branches of which are the same color as the pronotum, and the median stem is dark. Tergites brown. Sternites brown, with a white anterior patch.

Top of head with a number of long bristles and numerous short hairs

which, however, do not form a definite mat. Pronotum and wing stubs with many long bristles and short hairs. Tergites and sternites with medium long bristles on sides and scattered short bristles and hairs in middle with hairs overlapping onto the white portions along the posterior edge of each tergite. White lateral abdominal membrane of queen with numerous short hairs.

Head widely oval, upper side minutely rugose, with irregularities and muscle insertions in front. Fontanelle white, larger than ocellus and smaller than the light antennal base. Eye proportionately rather small. Ocellus with an elevated projecting upper margin of the head capsule and a small narrow white band on the head capsule at the lower margin of the ocellus. Ocellus very slightly more than its own length removed from the ocular suture, and the surface in a semi-vertical position. Postclypeus a little longer than half of its width. Antenna broken (15 articles intact), the third distinctly shorter than the fourth, the fourth distinctly shorter than the second. Mandibles similar to the worker mandibles of *A. angustatus* illustrated by Ahmad (1950, p. 69) so far as can be seen without dissection. Pronotum length about half of its width, and width slightly narrower than the head; front margin not indented, and hind margin shallowly indented, with a weakly lobed posterior margin. Hind margins of the mesonotum and metanotum widely emarginate, angles about 140 degrees to 150 degrees, posterior lobes rounded, posterior portion of lobes minutely rugose. Front coxa with a sharp longitudinal ridge with a fairly sharp projection with a peak angle in profile of about 135 degrees. Basal three tarsal joints with dark, widely rounded projections.

TABLE 2  
MEASUREMENTS (IN MILLIMETERS) OF MORPHOTYPE QUEEN OF  
*Apicotermes holmgreni*, NEW SPECIES

Width of head . . . . .	1.81
Length of postclypeus . . . . .	0.49
Width of postclypeus . . . . .	0.85
Diameter of eye . . . . .	0.46
Eye from lower margin . . . . .	0.13
Length of ocellus . . . . .	0.16
Width of ocellus . . . . .	0.09
Ocellus from eye . . . . .	0.16
Length of fontanelle . . . . .	0.18
Width of fontanelle . . . . .	0.15
Length of pronotum . . . . .	0.89
Width of pronotum . . . . .	1.78
Length of hind tibia . . . . .	1.99

Tibial spurs 3:2:2. The left hind leg has only one spur, an abnormality not previously observed by the author. Abdominal spiracles close to the side margins of the tergites. The sixth sternite of the queen with fairly long sides and forming an angle with the hind margin; hind margin distinctly bilobed in the middle.

COMPARISONS: *Apicotermes trögårdhi* cotype dealate from Mkosi, Zululand, is a lighter brown without such a sharp contrast with the white structures. White spots at base of bristles and hairs a little more conspicuous, particularly on the pronotum. Texture of head and sculpturing in front of the fontanelle is similar. Hump above the ocellus similarly raised. Ocellus proportionately farther from the eye. Elongate white spot in front of ocellus similar. Postclypeus quite similar in proportions. Antennal articles similar in proportional lengths. Pronotum proportionately narrower, with less angular indentation of hind margin. Hind lobes of mesonotum a little sharper and more angular; median indentation with a similar angle. Metanotum closely similar. Front coxal projection from the sharp ridge not so prominent or so sharp. Tarsal under pads similar in shape but not dark and not in such contrast with the rest of the tarsus. The enlarged sixth sternite of the female is proportionately somewhat longer, but the rather long sides form an angle with the hind margin that is indistinctly bilobed in the middle. On the whole these species are closer to each other than to any other species now known.

*Apicotermes arquieri* imago from Bas Uele, Belgian Congo (latitude 4° 21' N., longitude 25° 46' E.), has a smoother and more glossy surface of the less minutely rugose head than that of *A. holmgreni*. The head and postclypeus are wider. The postclypeus is about half as long as wide. Ocellus longer, but the general proportions and relation to the eye are similar. There is no elongate light mark immediately in front of the ocellus. Pronotum proportionately shorter and wider, but margins similar. Hind margin of the mesonotum much more deeply emarginate, angle close to a right angle or a little wider than a right angle. Front coxal ridge with a less prominent and less sharp projection. Tarsal under pads of similar shape but not so dark. The enlarged sixth sternite of the female is more triangular in shape, with narrower rounded sides not forming an angle with the hind margin, and hind margin not so distinctly bilobed in the middle. There is no doubt that *A. trögårdhi* is closer to *A. holmgreni* than is *A. arquieri*.

*Apicotermes desneuxi* morphotype queen from the Inkisi region, Belgian Congo, was not directly compared. From the description (Emerson, 1953, p. 108) it may be assumed that *A. holmgreni* is more closely related to *A. trögårdhi* and to *A. arquieri* than to *A. desneuxi*.

**SOLDIER (FIG. 6):** Head and pronotum yellowish. Apical portion of mandibles dark. Legs same color or slightly paler than the pronotum. Abdomen paler than pronotum.

Numerous bristles on top and sides of head and more abundant in front than in the rear. Postmentum with four bristles on the sides of the anterior portion; otherwise bare. Sides of bases of mandibles with a few

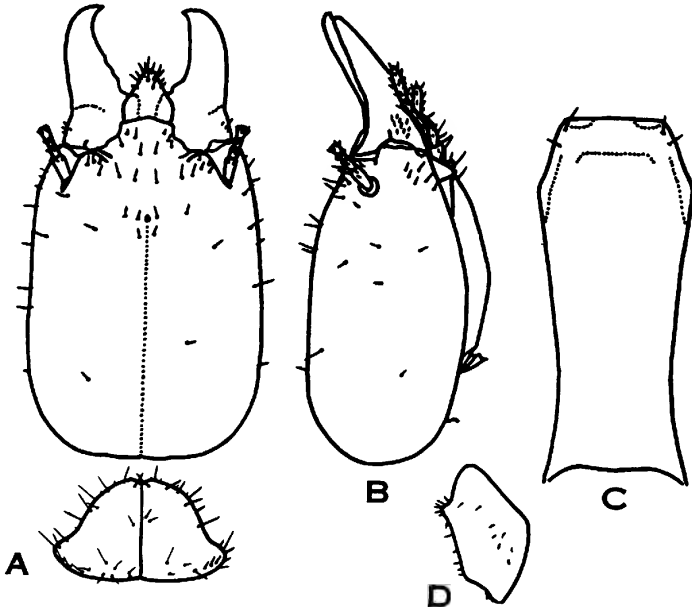


FIG. 6. *Apicotermes holmgreni*, new species, holotype soldier, near Nsakar Hill, Nyasaland. A. Head and pronotum from above. B. Head from the side. C. Enlarged postmentum from below. D. Coxa of foreleg showing profile of ridge.

short hairs. Labrum with a tuft of stiff bristles at the anterior end. Pronotum with scattered bristles, particularly around the margins; front margin with a few short hairs. Tergites with fairly long scattered hairs and slightly longer and stiffer marginal bristles. Sternites with hairs and bristles somewhat longer than those of tergites.

Head moderately large and thick, with fairly straight and parallel sides converging slightly towards the front (fig. 6A); hind margin somewhat rounded; front slightly depressed and joining the vertex with a slightly convex outline in profile (fig. 6B), but without an angular hump; front with small irregularities between the opening of the frontal gland and the base of the mandibles, but not so conspicuously irregular as in *A. desneuxi*; small hump or rounded ridge above the base of the antenna slightly more elevated in profile than in *A. desneuxi*. Postmentum from

below somewhat constricted in the posterior third (fig. 6C). Sides of labrum converging towards the front, with convex sides at base and slightly concave sides near tip; tip light and rounded, wider than in *A. desneuxi*. Antenna with 14 articles, the third shorter than the fourth, the fourth shorter than the second and equal to the fifth. Mandibles moderately robust, with characteristic dentation of the genus; tips more hooked than in *A. desneuxi*. Pronotum (fig. 6A) comparatively narrow compared to that of *A. desneuxi*, without the flared lateral sections as in *A. desneuxi*; front margin narrowly indented in front; hind margin slightly emarginate; profile in general concave but with straight or very slightly convex middle portion in contrast to the evenly concave profile of *A. desneuxi*. Front coxa with a conspicuous tooth-like projection of the sharp longitudinal ridge (fig. 6D). Tibial spines 3:2:2; the outer spine near the tip of the front tibia proportionately smaller than that of *A. desneuxi*.

TABLE 3  
MEASUREMENTS (IN MILLIMETERS) OF HOLOTYPE SOLDIER OF  
*Apicotermes holmgreni*, NEW SPECIES

Length of head with mandibles . . . . .	4.27
Length of head to side base of mandibles . . . . .	3.17
Width of head . . . . .	2.23
Thickness of head . . . . .	1.65
Widest width of postmentum . . . . .	0.75
Narrowest width of postmentum . . . . .	0.53
Length of left mandible . . . . .	1.62
Length of pronotum . . . . .	0.94
Width of pronotum . . . . .	1.62
Length of hind tibia . . . . .	1.82

COMPARISONS: *Apicotermes trågårdhi* cotype soldier from Mkosi, Zululand, differs in the slightly darker color of the preserved specimen, but it is suspected that the color may be the same in life. The pilosity of the head, thorax, and abdomen is so similar that no distinctions can be detected. The head is about the same length, but is proportionately narrower. The front irregularities are very closely similar, but *A. holmgreni* has a slightly more depressed front with slightly higher and more sharply rounded ridges above the bases of the antennae. From above the edges of these, ridges bulge laterally behind the top mandible joint, making a more rounded line than in *A. holmgreni*. The profile of the head at the junction of the front and vertex is closely similar, but *A. trågårdhi* is very slightly more angulate. Widest width of postmentum 0.66 mm.



Narrowest width of postmentum 0.41 mm. The postmentum is actually narrower and more slender and also proportionately more constricted in the posterior third. Proportion of the first to fifth antennal articles similar. Labrum similar in proportions. Mandibles very close in absolute size and shape, particularly the hook at the tip. Shape of pronotum very close, but *A. trågårdhi* is a little smaller and is proportionately a little shorter; angle and depth of the indentation in front very close; profile very close. The outer spine at the end of the front tibia is proportionately small in both species, but is somewhat smaller in *A. trågårdhi*. The tooth-like projection of the sharp ridge on the front coxa is proportionately a little smaller in *A. trågårdhi* but is otherwise close. *Apicotermes holmgreni* and *A. trågårdhi* form a related pair of species, with a series of morphological resemblances in both the soldier and imago that set them somewhat apart from the other species of the genus so far described.

*Apicotermes arquieri* paratype soldier from Bossembélé, French Equatorial Africa, has a similar pilosity of the tergites. The head is distinctly more converging towards the front in some specimens. The front of the head is very similar in the shape of the depression and the angle with the vertex. The head is proportionately wider, and the rounded ridge from the base of the antenna to the base of the mandibles is laterally more rounded when viewed from above. The postmentum has a more narrowly constricted posterior third. The labrum has a narrower tip. The mandibles are longer, but the curvature and proportions are close. The long tooth between the first small blunt tooth of the right mandible and the third sharp marginal tooth is more elongated and not so sharply pointed. *Apicotermes trågårdhi* and *A. holmgreni* are more closely related in this particular. *Apicotermes arquieri* has a similar hooked tip of each mandible. The pronotum is very close and undoubtedly shows affinity; the front margin has a very slightly wider-angled indentation, and the sides of the frontal lobe are slightly more rounded. Neither species has the flared lateral portions of the pronotum characteristic of *A. desneuxi* and its allied species. The major difference is in the profile of the pronotum which has a deeper-angled depression in the posterior portion, with a small convex hump at the front of the posterior portion just behind the frontal lobe. The projection on the front coxal ridge is very close but in profile is less concave from the tip of the tooth-like projection towards the junction with the trochanter. The front tibial spines are similar.

*Apicotermes lamani* paratype soldier from the type colony, "Madzia Distrikt, Fr. Kongo," is larger; has a less distinctly constricted postmentum in the posterior third; has a slightly narrower tip of the labrum; has a wider pronotum with more flaring sides and a wider-angled an-

terior indentation; has a blunter, tooth-like projection on the front coxa; has fewer short hairs on the tergites; and has a proportionately larger outside spine on the front tibia. *Apicotermes lamani* shows a resemblance in the shape of the mandibles at the tip, in the parallel sides of the head, in the front shallow depression and the profile of the junction of the front and vertex, and in having a tooth-like projection on the sharp ridge of the front coxa even though it is more blunt and less conspicuous than in *A. holmgreni*. Although the postmentum is different, it shows some relationship in the narrowest portion about two-thirds of its length from the front portion.

**DISTRIBUTION AND ECOLOGY:** The single holotype soldier and the single morphotype queen were collected by W. A. Sands and W. Wilkinson, August 23, 1953, No. 188, near Nsakarú Hill on Namwera Road, Nyasaland, in low hard gray mounds in *dambo* grassland with trees. There is no indication on the attached label of the details of the nest structure from which this queen and soldier were taken. W. V. Harris (personal communication) informs me that no special type of nest was noted by the collectors. The term "*dambo*" is equivalent to the term "*dembo*" used in the Katanga, Belgian Congo, for seasonal swampy areas within the wooded grasslands. The holotype and morphotype are deposited in the British Museum (Natural History). The species is named in honor of Prof. Nils Holmgren of the University of Stockholm who first named the genus *Apicotermes* and whose pioneer studies on the phylogeny of termite genera set the stage for our present classification. Largely through the efforts of Professor Holmgren and the late Prof. F. Silvestri, the phylogeny of termites has attained a maturity probably not matched by that of any other order of insects.

*Apicotermes arquieri* Grassé and Noirot

**IMAGO:** The specimens conform in general to the description by Grassé and Noirot (1954) and to the generic description (Emerson, 1953). The fontanelle is white, triangular, and large. The antennal articles number 16; the third is small and equal to or shorter than the fourth, and the fourth is shorter than the second. The profile of the front coxa is with or without a very slight, flatly rounded projection from the sharp ridge. The metanotum of the female has a rather rounded posterior indentation, forming an angle of about 90 degrees.

**COMPARISONS:** *Apicotermes trågårdhi* female has a narrower oval fontanelle. The color is similar. The general proportions of the head, ocelli, eyes, and fontanelle are fairly close, but *A. trågårdhi* is smaller in the female sex. The pronotum is absolutely and proportionately nar-

rower, but the indentations of both the front and hind margins are closely similar. The front coxa is similar. The metanotum is much less incised, with an angle of about 157 degrees. The enlarged sixth sternite of the female is very similar; the softer anterior parts are more distinct, but this is probably because of the preservation; the sides are a little more straight and the hind lateral angles are a bit less curved than in *A. arquieri*.

TABLE 4  
MEASUREMENTS (IN MILLIMETERS) OF IMAGO OF *Apicotermes*  
*arquieri* GRASSÉ AND NOIROT

	Male	Female
Width of head . . . . .	1.83	2.02
Length of postclypeus . . . . .	0.50	0.43
Width of postclypeus . . . . .	0.85	0.92
Diameter of eye . . . . .	0.41	0.45
Ocellus from eye . . . . .	0.18	0.18
Length of ocellus . . . . .	0.17	0.22
Length of fontanelle . . . . .	0.18	0.18
Width of fontanelle . . . . .	0.18	0.22
Length of pronotum . . . . .	0.68	0.85
Width of pronotum . . . . .	1.58	1.88
Length of hind tibia . . . . .	2.09	2.18
Length of forewing from costal suture . . . . .	—	19.13
Width of forewing . . . . .	4.57	4.70

*Apicotermes desneuxi* morphotype queen is lighter in color. The pilosity of the head, pronotum, and abdomen is similar. The fontanelle is oval. The postclypeus is shorter. The head is in general smaller, but the proportions of the ocelli and eyes are similar. The pronotum is narrower, but the indentations are similar. The coxa in profile has less protuberance of the sharp ridge. The notch of the metanotum is less angular and rounded, with an angle of about 120 degrees. The side angles of the sixth sternite are about the same.

**NYMPH:** Mandibles like the drawing of *A. angustatus* in Ahmad (1950) except that the teeth are a bit sharper and the left mandible has a more pronounced undulation of the cutting edge of the first plus second marginal tooth like the drawing of *A. occultus* by Silvestri (1914, fig. 15). Possibly the mandible drawn by Ahmad was slightly worn. The general proportions are similar.

**SOLDIER:** Conforms to the generic description in Emerson (1953).

One soldier has four anterior bristles on the postmentum, a close pair near the anterior lateral margin on each side. Another soldier has two postmental bristles as is usual for the genus. The tergites have bristles and also a number of hairs about one-half of the length of the bristles. Sides of head fairly straight and slightly convex. Postmentum definitely narrower in the middle than at the front end. Front margin of the pronotum definitely but slightly indented, with the angle wide and shallow; hind margin barely emarginate, with a very wide shallow indentation that is almost straight. Profile of front coxa with a prominent rounded projection of the sharp longitudinal ridge. Tibial spurs 3:2:2. Outer spur of the fore tibia on the right leg of one soldier small, and on the left leg of the same soldier almost as long as the inner spurs.

TABLE 5  
MEASUREMENTS (IN MILLIMETERS) OF FIVE SOLDIERS OF *Apicotermes*  
*arquieri* GRASSÉ AND NOIROT

	Bas Uele, Belgian Congo	Paratype, Bossembélé, French Equatorial Africa
Length of head with mandibles . . . . .	3.96-4.39	4.27
Length of head to side base of mandibles . . . . .	2.74-3.17	2.93
Width of head . . . . .	2.21-2.45	2.48
Thickness of head . . . . .	1.50-1.71	—
Widest width of postmentum . . . . .	0.73-0.82	—
Narrowest width of postmentum . . . . .	0.43-0.47	—
Length of left mandible . . . . .	1.65-1.79	1.75
Length of pronotum . . . . .	0.76-0.83	—
Width of pronotum . . . . .	1.50-1.71	1.64
Length of hind tibia . . . . .	1.85-2.06	2.17

COMPARISONS: *Apicotermes arquieri* is very close to the description and figures of *A. occultus* (Silvestri, 1914, p. 29, figs. 15, 16). The head of *A. occultus* seems to have straighter and more parallel sides than in most specimens of *A. arquieri*. There is some variation in the size of the head and relative degree of convergence towards the front in several soldiers of a homotype colony of *A. arquieri* from Bas Uele, Belgian Congo (latitude 4° 21' N., longitude 25° 47' E.). In a colony from Digba, Uele, Belgian Congo, there is an exact match to the shape of the head of *A. occultus* drawn by Silvestri (1914, fig. 15). Silvestri gives the width of the head of the soldier of *A. occultus* as 2.25 mm. *Apicotermes ar-*

*quieri* head widths are 2.19, 2.19, 2.31, and 2.45 mm. for the Bas Uele colony, and 2.48, 2.53, and 2.56 mm. for the paratype colony from Bossembélé. Aside from this variation in the size of the head, these two colonies match very closely. Some of Silvestri's measurements of *A. occultus* (i.e., length of head and length of mandible) are probably from different anatomical points than those in the present paper. The front margin of the pronotum of *A. occultus* seems to have a wider-angled front indentation, but the flared lateral portions seem to be absent in both *A. occultus* and *A. arquieri*. The wider indentation may well be due to the position of the pronotum as drawn. The position is doubtless with a more vertical frontal lobe than in the drawings of the pronota in Emerson (1953, fig. 2). The indication of a hump in figure 16 (Silvestri, 1914) in the portion just behind the base of the frontal lobe is suggestive of a shape similar to that of *A. arquieri*. The front coxa is similar.

The nests of the two species differ (Desnoux, 1953; Grassé and Noirot, 1954; Schmidt, 1955a) and indicate ethological distinction. The two species may be another example of a pair of ethospecies, but a careful comparison of properly identified specimens may reveal distinctive anatomical characters in the soldiers that are not described as yet. The two species are very close in their structure and may prove to be difficult to separate by morphological traits. The nest assigned in the literature to *A. occultus* is quite distinct from that of *A. arquieri* although related. This nest, however, has no associated specimens and is assigned to this species on the basis of its locality. However, it seems reasonable to suppose that the nest does belong to *A. occultus*. The nests of both *A. occultus* and *A. arquieri* exhibit a remarkable case of vestigial behavior, although the ancestral type of nest is not known (Schmidt, 1955a).

*Apicotermes trågårdhi* cotype from Mkosi, Zululand, has similar pilosity, particularly on the tergites. The tooth of the right mandible is slightly less prominent, and the angle between the second and third teeth near the base is wider. The tip of the left mandible is a little more hooked. The head is proportionately narrower, with slightly straighter sides. The anterior portion of the postmentum is proportionately narrower, and the middle constriction is somewhat less marked. The front coxa has a more pointed but much less prominent projection from the sharp longitudinal ridge. The pronotum is proportionately narrower; the front margin has a narrower but equally shallow indentation; and the hind margin is straight, without even a shallow indentation. Next to *A. occultus*, *A. trågårdhi* and *A. holmgreni* are the closest species to *A. arquieri* on the basis of the pilosity and the postmentum. *Apicotermes arquieri* is, however, closer to *A. lamani* in the front coxa.

*Apicotermes lamani* from Luki, Belgian Congo, has shorter and less abundant hairs on the tergites. The head is proportionately longer. The postmentum is longer, with less abrupt constriction behind the anterior portion. The mandibles are more robust, wider, and longer, with the tooth of the right mandible less prominent and the inside edge of the left mandible less curved towards the tip. The pronotum has deeper indentations in both the front and hind margins and is also proportionately wider. The front coxa has a less prominent projection, with a more sloping basal margin in profile, but the general type is close.

*Apicotermes desneuxi* holotype from the Inkisi region, Belgian Congo, has shorter and less abundant hair in the middle of the tergites. The sides of the head are somewhat straighter in the middle. The postmentum is much wider in the middle, with only a slight constriction behind the anterior portion. The pronotum has more rounded front side angles and is proportionately wider; front margin with a wider and very shallow emargination and the hind margin more indented. The front coxa has a rounded longitudinal sharp ridge in profile, with a much less prominent projection than in *A. arquieri*.

*Apicotermes kisantuensis*, *A. angustatus*, and *A. porifex* are related to *A. desneuxi* and *A. gurgulifex*. All differ markedly from *A. arquieri* in the shapes of the postmenta and pronota (Emerson, 1953, figs. 1, 2, 4B).

DISTRIBUTION AND ECOLOGY: The descriptions are drawn from five homotype soldiers collected with 12 mature imagoes and some abnormal imagoes with incompletely developed wings together with workers from a nest studied by J. Desneux, latitude 4° 21' N., longitude 25° 47' E., Bas Uele, Belgian Congo. These soldiers were compared with paratype soldiers from Bossembélé, French Equatorial Africa, determined and collected by Pierre-P. Grassé and Charles Noirot. Also soldiers from Digba, Uele, Belgian Congo, August, 1953, and determined by J. Desneux as "*Apicotermes uelensis*" belong to this species. All records of *A. arquieri* are from localities in savannas.

#### *Apicotermes* species

IMAGO: Color more yellow-brown than that of *A. holmgreni*, particularly in the more yellowish brown postclypeus and labrum. Light dots at the base of the bristles and hairs similar. Pilosity of the head and pronotum similar. Compared to *A. holmgreni*, the top of the head is more smooth and glossy. The size of the fontanelle and the relation of ocelli and eyes are close. The eye is slightly smaller and a little farther from the ocellus. The elongated white spot immediately in front of the ocellus in *A. holmgreni* is absent in this specimen. Antennal articles similar in pro-

portion to those of *A. holmgreni*. Postclypeus proportionately shorter. Pronotum wider in relation to length. Angles of hind margins of mesonotum and metanotum a little sharper. Band of rugosity on the posterior portion of the mesonotum longer. Rounded pads at the lower tips of the first, second, and third tarsal segments white and not such a contrasting dark. Sharp ridge of front coxa evenly convex in profile without a conspicuous projection. Fore tibia from the side conspicuously swollen or thicker at the apical end compared to the basal portion; similar in both species. Tibial spurs 3:2:2.

TABLE 6  
MEASUREMENTS (IN MILLIMETERS) OF FEMALE DEALATE OF  
*Apicotermes* SPECIES

Length of head to side base of mandibles . . . . .	1.32
Length of head to front of postclypeus . . . . .	1.53
Width of head . . . . .	1.81
Length of postclypeus . . . . .	0.31
Width of postclypeus . . . . .	0.85
Diameter of eye . . . . .	0.41
Eye from lower margin . . . . .	0.14
Length of ocellus . . . . .	0.17
Width of ocellus . . . . .	0.13
Ocellus from eye . . . . .	0.20
Length of fontanelle . . . . .	0.20
Width of fontanelle . . . . .	0.18
Length of pronotum . . . . .	0.88
Width of pronotum . . . . .	1.82
Length of hind tibia . . . . .	1.94

COMPARISONS: The single specimen conforms to the generic characters of *Apicotermes*. *Apicotermes arquieri* and *A. trågårdhi* have a more projecting ridge of the front coxa. The front coxa and the proportions of the pronotum are close to those of *A. desneuxi*, but *A. desneuxi* is smaller in nearly every measurement.

DISTRIBUTION AND ECOLOGY: The description is taken from a single dealate female collected by A. Emerson at Yangambi, Belgian Congo, May 30, 1948, with dealates of several other genera from the surface layers of termite mounds and logs in the rain forest. The species is distinct from the known imagoes of *A. trågårdhi*, *A. holmgreni*, *A. arquieri*, and *A. desneuxi*. The imagoes of *A. occultus*, *A. lamani*, *A. gurgulifex*, *A. kisantuensis*, *A. angustatus*, and *A. porifex* are unknown. The Yangambi specimen might conceivably belong to any of the rain-forest species. Under the circumstances it is deemed unwise to give a name to

this specimen until associated soldiers are found or the imagoes of the forest species have been discovered.

*Allognathotermes aburiensis* (Sjöstedt), new combination

*Apicotermes aburiensis* SJÖSTEDT, 1926, p. 3 (soldier).

*Apicotermes aburiensis* SNYDER, 1949, p. 149 (synonymy).

*Apicotermes aburiensis* EMERSON, 1953, p. 117 (soldier).

An examination of a cotype soldier lent by the British Museum and a paratype soldier exchanged with the Stockholm Museum makes it quite clear that this species from Aburi, Gold Coast, was erroneously assigned

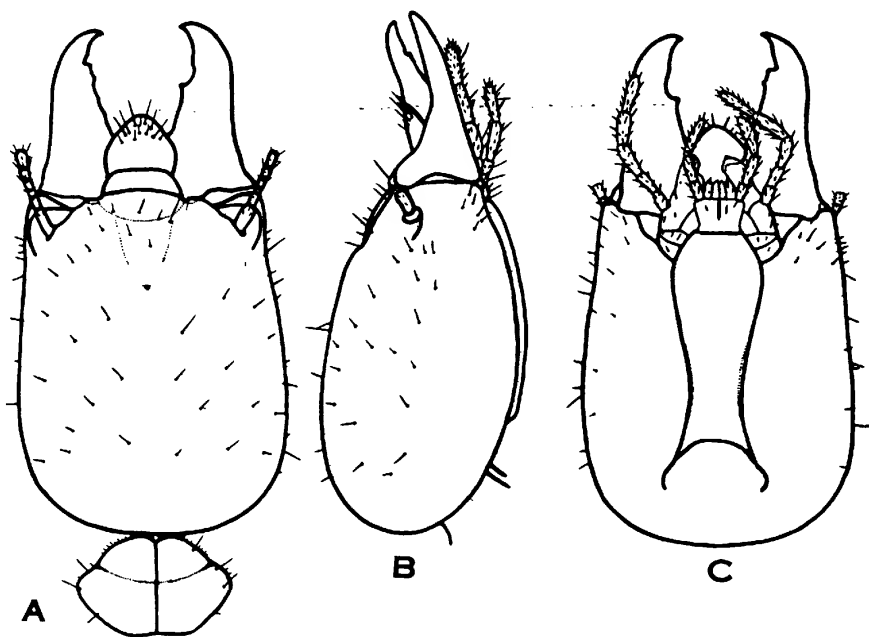


FIG. 7. *Allognathotermes hypogeus* Silvestri, cotype soldier, Kakoulima, French Guinea. A. Head and pronotum from above. B. Head from the side. C. Head from below.

to the genus *Apicotermes* by Sjöstedt, and the original description did not mention the characters that might have enabled subsequent authors to reassign the species to *Allognathotermes* Silvestri (Silvestri, 1914, p. 31; Emerson, 1953, p. 103; Grassé and Noirot, 1954, pp. 378–380).

**SOLDIER:** The pilosity of the head is close to that of *A. hypogeus* (fig. 7), but the bristles on top at the rear of the head are not so long. The



TABLE 7  
MEASUREMENTS (IN MILLIMETERS) OF SOLDIERS OF *Allognathotermes*

	<i>A. aburiensis</i> Paratype, Aburi, Gold Coast	<i>A. hypogaeus</i> Cotype, Kakoulima, French Guinea	<i>A. hypogaeus</i> , Adiopodoumé, Ivory Coast	<i>A. morensis</i> Paratype, Ferkessedougou, Ivory Coast
Length of head with mandibles . . . . .	4.02	—	—	4.07
Length of head to side base of mandibles . . . . .	2.79	2.65	2.65	2.80
Width of head . . . . .	1.97	2.12	1.94	1.97
Widest width of postmentum . . . . .	0.69	—	—	0.70
Narrowest width of postmentum . . . . .	0.53	—	—	0.52
Length of left mandible . . . . .	1.60	—	1.53	1.65
Length of pronotum . . . . .	0.74	0.68	0.74	0.71
Width of pronotum . . . . .	1.35	1.24	1.38	1.35
Width between peaks of front lobes of pronotum . . . . .	0.35	—	—	0.21
Length of hind tibia . . . . .	1.47	1.50	1.41	1.47

head is more elongate than that of *A. hypogeus* and has straighter sides converging somewhat towards the front in a manner close to that in *A. ivorensis* Grassé and Noirot (1954, fig. 15). *Allognathotermes hypogeus* cotype soldier (fig. 7) from Kakoulima, French Guinea, has slightly straighter sides than specimens from Adiopodoumé, Ivory Coast, but the difference is not considered to have taxonomic significance. The antenna of *A. aburiensis* has 14 articles. The mandibles are close to those of *A. hypogeus*, except that the first marginal tooth of the left mandible is smaller, and the angle with the apical cutting edge is much more shallow and wide. *Allognathotermes hypogeus* and *A. ivorensis* are close in this character. The postmentum is longer than in *A. hypogeus*, with straighter sides between the front portion and the constriction. The width of the constriction is the same as in the Adiopodoumé specimens of *A. hypogeus* and is markedly less constricted than in the paratype soldier and in the drawing of *A. ivorensis*. The paratype soldier has a postmentum with a somewhat longer portion in front of the constriction which is one-eighth of the length of the postmentum from the middle posterior margin. The front coxa is virtually identical in *A. hypogeus* and *A. aburiensis*. The most marked specific character is in the front margin of the pronotum. In both *A. hypogeus* and *A. ivorensis* the mid-indentation is narrower and sharper, with the peaks of the front margin close together in front, while in *A. aburiensis* the indentation is less sharp and wider, with the peaks farther apart in front, and the angle of indentation is about 135 degrees.

**DISTRIBUTION AND ECOLOGY:** The description is based on two soldiers from the type colony determined by Y. Sjöstedt as *Apicotermes aburiensis*, Aburi, Gold Coast, collected by W. H. Patterson, 1926, from a mound 36 feet in circumference. The mound described was probably that of another termite secondarily occupied by galleries of *Allognathotermes aburiensis*.

The cotype soldier of *A. hypogeus* from Kakoulima, French Guinea, is in the Silvestri collection in the Scuola Agraria, Portici, Italy. Specimens of *A. hypogeus* from Adiopodoumé, Ivory Coast, and a paratype soldier and worker of *A. ivorensis* were kindly exchanged by Prof. P.-P. Grassé and Dr. Charles Noirot from their collection.

The imago of *A. hypogeus* and the soldier of *A. ivorensis* have been described by Grassé and Noirot (1954) with an interesting account of the nest structures of these species. Their figure 14C of the imago is labeled *Allognathotermes ivorensis* but probably is an imago of *A. hypogeus*, because they do not mention possessing an imago of *A. ivorensis*.

## PHYLOGENY OF SPECIES WITHIN THE GENUS *APICOTERMES*

Because of the detailed structure of the nests constructed by the workers of each species of *Apicotermes*, it would be very helpful to find anatomical correlations that would verify the phylogenetic order of the behavior manifestations (Schmidt, 1955a). I have been disappointed in finding only small and rather weak indications of phylogenetic order in the worker, soldier, and imago structures. It is true that a sound phylogenetic tree of species within a genus has not been constructed for any large genus of termites, but in the case of *Apicotermes*, such a tree is possible for the nest-building behavior, and much would be added to our understanding of the evolutionary processes involved if we could find adequate correlations of anatomy and behavior.

One can discern related pairs of species on the basis of anatomical structure, and these pairs in every known case also show close relationships of the nest structures. The related pairs now known are *Apicotermes trögårdhi* and *A. holmgreni*, *A. arquieri* and *A. occultus*, *A. gurgulifex* and *A. desneuxi*, *A. kisantuensis* and *A. angustatus*, and *A. angustatus* and *A. porifex*. This leaves only *A. lamani* not included in a related pair.

Emerson (1953, p. 103) concluded that *Allognathotermes* was the closest genus to *Apicotermes* and should be considered somewhat more primitive. This is still probably the best hypothesis, but the ingenious work of Grassé and Noirot (1954) on the detailed anatomy of the intestine makes it questionable whether *Allognathotermes* should be placed in front of *Apicotermes*. Grassé and Noirot do not draw precise phylogenetic conclusions from their study, but it is difficult for the present author to recognize a more primitive condition of the valves of the intestine in *Allognathotermes* from their figures and descriptions. The contrary would seem most probable, but the phylogenetic significance of the new characters discovered by Grassé and Noirot needs further evaluation. The author has not directly examined the intestinal anatomy as yet, but he hopes to follow this promising suggestion in the future. At the moment it would seem best to consider *Allognathotermes* and *Apicotermes* related genera derived from an unknown genus with the primitive characters of each genus.

The nest constructions of *Allognathotermes hypogeus* and *A. ivorensis* are described by Grassé and Noirot (1954, pp. 357–358) and question that the ethology of *Allognathotermes* is more primitive than pared to those of other genera also related to *Apicotermes*. There is no

that of *Apicotermes*, but it is not yet possible to determine the phylogenetic order of the detailed ethology of all the related genera, although all exhibit similar general characteristics of nest and gallery construction.

The workers of the following seven species of *Apicotermes* were available for study, and some characters were found promising for phylogenetic interpretation.

*Apicotermes lamani* from Luki, Bas Congo, Belgian Congo, has a front coxa with a prominently arched, sharp, tooth-like ridge with about 14 short but not markedly conspicuous spines on the ridge. The insides of the bases of the femur and the trochanter of the front leg have stiff hairs; one on the base of each femur is very long but not so robust, dark, or conspicuous as the tibial spines. The tibia is swollen and possesses many irregularly spaced, long, prominent, and conspicuous spines on the inside and sides of the outer two-thirds.

*Apicotermes arquieri* from Digba, Uele, Belgian Congo, is related to *A. trögårdhi*. The sharp ridge of the front coxa is larger in proportion than in *A. lamani*. About 17 spines occur on the ridge, but are not markedly robust or conspicuous. The shape of the front coxa is very close to that of *A. occultus* as drawn by Silvestri (1914, fig. 17). The tibial and femoral spines or stiff hairs are not very conspicuous or robust. The tibial spines are shorter than those of *A. lamani* but are about as thick as and a little more robust than the spines at the base of the femur.

*Apicotermes trögårdhi* from Mkosi, Zululand, is fairly close to *A. arquieri*. The projection of the front coxal ridge is more tooth-like and with a stronger curvature than in *A. arquieri*. The small spines on the ridge seem less numerous and rather inconspicuous. The tibial spines are shorter than those of *A. lamani*, and the femoral spines are more hair-like and inconspicuous. The tibial spines are robust and distinct.

*Apicotermes gurgulifex* from Lunda, Angola, is in poor condition for study, but seems to match *A. lamani* fairly well.

*Apicotermes desneuxi* from the Inkisi region of the Belgian Congo is similar to *A. lamani* in the spines and proportions, but the sharp front coxal projection is a little smaller.

*Apicotermes angustatus* from Kondue, Belgian Congo, has a slightly smaller sharp ridge than that of *A. lamani*, but is otherwise very close.

*Apicotermes porifex* from Luluabourg, Belgian Congo, is similar in all details to *A. lamani*.

It may be seen from the above comparisons that the workers of *Apicotermes* fall into two groups of related species. *Apicotermes trögårdhi*, *A. arquieri*, and *A. occultus* are included in one group, and *A.*

*lamani*, *A. gurgulifex*, *A. desneuxi*, *A. angustatus*, and *A. porifex* compose another group.

On the basis of the external anatomy, the soldier of *Allognathotermes* may be considered the relatively more primitive of the two genera with our present knowledge. If this be so, *Apicotermes trågårdhi*, with its narrow pronotum and constricted postmentum, seems to be the most primitive species of its genus. Because of the shared constricted postmenta, I am inclined to place *A. trågårdhi*, *A. holmgreni*, *A. arquieri*, and *A. occultus* in one branch of the phylogenetic tree, and *A. gurgulifex*, *A. desneuxi*, *A. kisanuensis*, *A. angustatus*, and *A. porifex* in another main branch. *Apicotermes lamani* seems to be related to the *A. trågårdhi*-*A. occultus* group in the soldier postmentum, and to the *A. gurgulifex*-*A. porifex* group in the worker legs. With the possible exception of *A. lamani*, the known nest structures fit well into such an arrangement, but with our present knowledge, we are not yet in a position to draw any final conclusions, and the proposed phylogenetic trees must remain tentative until much more information has been accumulated. In spite of the inconclusive detailed phylogenetic arrangement of the species, however, a remarkable general parallelism between the evolution of behavior and the evolution of anatomical structure is apparent, and the principles set forth by Schmidt (1955a) seem fairly well substantiated. An outline of hypotheses that suggest the possible order of existing data is valuable as a base for comparison as new information is gathered.

### SUMMARY

1. *Apicotermes gurgulifex*, a new species from Angola, is described and primarily distinguished from its closest relative, *A. desneuxi*, by the structure of its nest.

2. *Apicotermes holmgreni*, a new species from Nyasaland, is described.

3. *Apicotermes arquieri* Grassé and Noirot is compared to other species and, with our present knowledge, is shown to be only ethologically distinct from *A. occultus* Silvestri.

4. The species described as *Apicotermes aburiensis* Sjöstedt is transferred to *Allognathotermes aburiensis* (Sjöstedt), new combination.

5. The terms "ethospecies" and "ethotype" are suggested for species and races primarily distinguished by their instinctive behavior.

6. The concept of the "species" is discussed particularly as it applies to "ethospecies" and to "physiological species."

7. The phylogeny of instinctive behavior among species of *Apicotermes* is substantiated.

## LITERATURE CITED

ADRIAANSE, A.

1948. *Ammophila campestris* Latreille und *Ammophila adriaansei* Wilche. ein Beitrag zur vergleichenden Verhaltensforschung. Behaviour, vol. 1, pp. 1-35.

AHMAD, M.

1950. The phylogeny of termite genera based on imago-worker mandibles. Bull. Amer. Mus. Nat. Hist., vol. 95, pp. 37-86.

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK, AND K. P. SCHMIDT

1949. Principles of animal ecology. Philadelphia and London, W. B. Saunders Co., 837 pp., 263 figs.

BORGMEIER, T.

1950. Neue Gattungen und Arten termitophiler Staphyliniden aus Brasilien, nebst einem Katalog aller bisher aus der neotropischen Region beschriebenen Arten (Col. Staph.). Rev. Ent., vol. 21, pp. 625-676.

DESNEUX, J.

1918. Un nouveau type de nids de termites. Rev. Zool. Africaine, vol. 5, pp. 298-312.
1948. Les nidifications souterraines des *Apicotermes*, Termites de l'Afrique tropicale. Rev. Zool. Bot. Africaines, vol. 41, pp. 1-54.
1953. Les constructions hypogées des *Apicotermes* termites de l'Afrique tropicale. Ann. Mus. Roy. Congo Belge, Sci. Zool., sér. 8<sup>e</sup>, vol. 17, pp. 1-98 (May, 1953).

EMERSON, A. E.

1935. Termitophile distribution and quantitative characters as indicators of physiological speciation in British Guiana termites (Isoptera). Ann. Ent. Soc. Amer., vol. 28, pp. 369-395.
1938. Termite nests. A study of the phylogeny of behavior. Ecol. Mongr., vol. 8, pp. 247-284.
1945. Taxonomic categories and population genetics. Ent. News, vol. 56, pp. 14-19.
1952. The supraorganismic aspects of the society. In Structure et physiologie des sociétés animales. Colloques internationaux du Centre National de la Recherche Scientifique. Paris, no. 34, pp. 333-354.
1953. The African genus *Apicotermes* (Isoptera: Termitidae). Ann. Mus. Roy. Congo Belge, Sci. Zool., sér. 8<sup>e</sup>, vol. 17, pp. 99-121 (May, 1953).
1955. Biological species. In Species. Encyclopaedia Britannica. Chicago.

GRASSÉ, P.-P.

1952. Le polymorphisme des termites et la détermination des castes. Trans. 9<sup>e</sup> Internl. Congr. Ent., vol. 1, pp. 51-62.

GRASSÉ, P.-P., AND C. NOIROT

1948. Sur le nid et la biologie du *Sphaerotermes sphaerotherax* (Sjöstedt). Ann. des Sci. Nat. Zool., ser. 11, vol. 10, pp. 149-166.
1954. *Apicotermes arquieri* (Isoptère): ses constructions, sa biologie. Considérations générales sur la sous-famille des *Apicotermitinae* nov. *Ibid.*, ser. 11, vol. 16, pp. 345-388.

LEHRMAN, D. S.

1953. A critique of Konrad Lorenz's theory of instinctive behavior. Quart. Rev. Biol., vol. 28, pp. 337-363.

LIGHT, S. F.

1942-1943. The determination of the castes of social insects. *Quart. Rev. Biol.*, vol. 17, pp. 312-326; vol. 18, pp. 46-63.

1944. Experimental studies on ectohormonal control of the development of supplementary reproductives in the termite genus *Zootermopsis* (formerly *Termopsis*). *Univ. California Publ. Zool.*, vol. 43, pp. 413-454.

LORENZ, K.

1941. Vergleichende Bewegungsstudien an Anatinen. *Jour. Ornith.*, vol. 89, pp. 194-294.

LÜSCHER, M.

1952. New evidence for an ectohormonal control of caste determination in termites. *Trans. 9<sup>o</sup> Internl. Congr. Ent.*, vol. 1, pp. 289-294.

MILLER, E. M.

1942. The problem of castes and caste differentiation in *Prorhinotermes simplex* (Hagen). *Bull. Univ. Miami*, vol. 15, pp. 1-27.

MULLER, H. J.

1942. Isolating mechanisms, evolution and temperature. *Biol. Symposia*, vol. 6, pp. 71-125.

SCHMIDT, R. S.

1955a. The evolution of nest-building behavior in *Apicotermes* (Isoptera). *Evolution*, vol. 9, pp. 157-181.

1955b. Termite (*Apicotermes*) nests—important ethological material. *Behaviour*, vol. 8, pp. 344-356.

SILVESTRI, F.

1914. Contribuzione alla conoscenza dei termitidi e termitofili dell'Africa occidentale. I. Termitidi. *Boll. Lab. Zool. Gen. Agr. Portici*, vol. 9, pp. 1-146.

SJÖSTEDT, Y.

1926. Neue Termiten aus der Goldküste. *Arkiv Zool.*, vol. 18B, no. 12, pp. 1-5.

SNYDER, T. E.

1949. Catalog of the termites (Isoptera) of the world. *Smithsonian Misc. Coll.*, vol. 112, pp. 1-490.

THORPE, W. H.

1940. Ecology and the future of systematics. In Huxley, J., *The new systematics*. Oxford, Clarendon Press, pp. 341-364.

TINBERGEN, N.

1951. *The study of instinct*. London, Oxford University Press.

TURESSON, G.

1922. The genotypical response of the plant species to the habitat. *Hereditas*, vol. 3, pp. 211-350.

WEIDNER, H.

1955. Über einige interessante Insekten (Lepidoptera, Orthoptera, Isoptera) aus Angola. *Ent. Zeitschr.*, no. 17, pp. 201-207.

